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RM-100

United States
Department of
Agriculture

Forest Service

Rocky Mountain
Forest and Range
Experiment Station

Fort Collins,
Colorado 80526

General Technical
Report RM-100

1983

Prediction of Wildlife and Fish Resources for National Assessments and Appraisals

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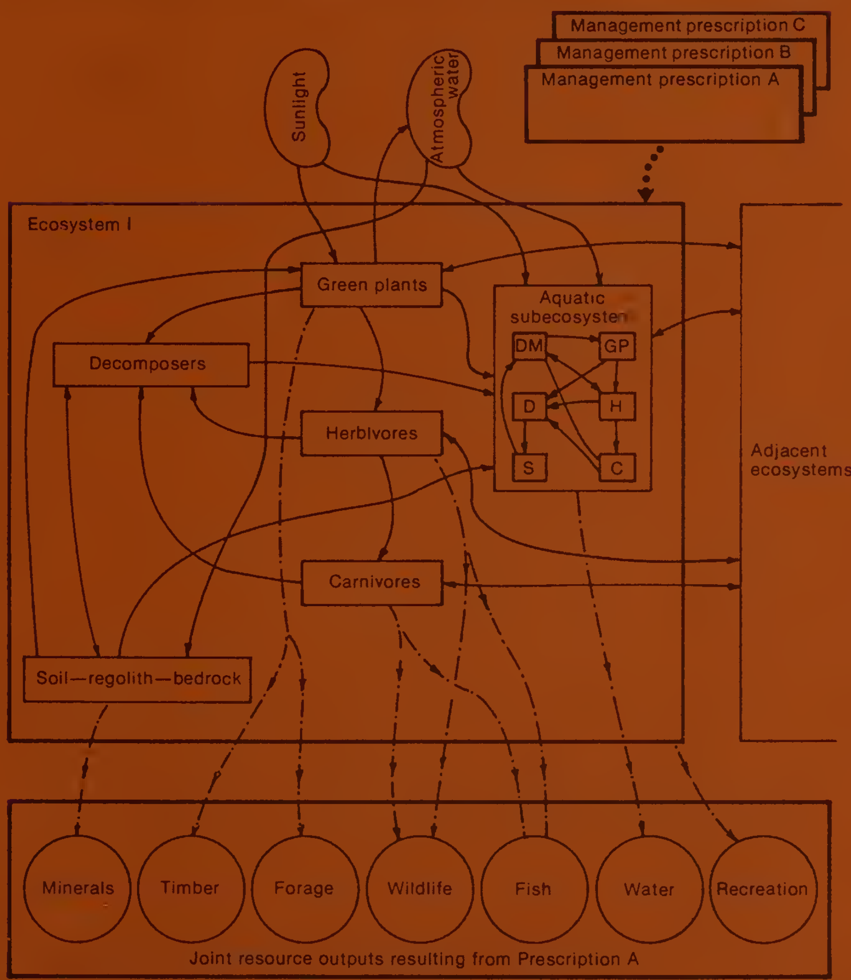

Abstract

The ecological analysis techniques discussed are useful in models to assess the renewable resources of the nation's forests, rangelands, agricultural lands, and associated waters. Outputs of the techniques are habitat quality, habitat quantity, population occurrence, population quantities, population age structure, population size structure, and population sex structure. Types of analytical techniques included are expert opinion, habitat quality indexes, regression analyses, multivariate analyses, pattern recognition procedure with Bayesian statistics, life table analyses, Leslie matrix analyses, and models of harvest, population dynamics, predator-prey, systems ecology, linear programing, linear equations, difference equations, and differential equations.

USDA Forest Service
General Technical Report RM-100

July 1983

Prediction of Wildlife and Fish Resources for National Assessments and Appraisals

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EXCHANGE Rec'd
NOV 26 1985

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Contents

Prediction of Wildlife and Fish Resources for National Assessments and Appraisals

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MANAGEMENT IMPLICATIONS

This overview of ecological analysis techniques for predicting—as contrasted with directly inventorying—wildlife and fish resources provides state, regional, and national analysts with a better understanding of the techniques available, for use in national assessments and appraisals, to predict wildlife and fish population occurrence, quantities, harvest quantities, and structure.

Although the techniques for predicting terrestrial wildlife are quite useful, they need to be made more biologically and ecologically complete and accurate. Many techniques use habitat variables to arrive at a habitat quality or suitability rating, usually expressed as an index of the habitat capability to produce wildlife. In most cases, models predict potential rather than actual population occurrence, quantity, or structure. Techniques that provide estimates of population levels are for relatively small areas and have rarely been tested in the field.

Techniques for predicting aquatic wildlife and fish habitat quality and population or harvest quantities in ponds, lakes, and oceans, while deficient because they require important biological and ecological assumptions that can not be entirely substantiated, are among the most mathematically rigorous analysis techniques. Many of the models to predict harvest quantities also provide estimates of sex ratios and numbers, age structure and numbers, or size structure and numbers. A few techniques for predicting habitat quality and population quantities in streams and rivers have been developed recently. Techniques to predict aspects of aquatic resources over time are rare. Most techniques are applicable only to small, site specific situations and to a single species rather than guilds; communities; or all the species, as a group, of entire ecosystems. Also, techniques exist only for a limited number of species. There presently are no techniques for predicting population occurrence only.

The accuracy of most of the techniques for predicting terrestrial and aquatic wildlife and fish is not discussed in this paper because there are no established standards by which to evaluate their accuracy.

The slow development of ecological analysis techniques for predicting wildlife and fish resources reflects the relatively incomplete understanding of ecosystem structure and function and of habitat relationships and intraspecies and interspecies interactions. Also, the relationship between population structure and habitat variables are poorly understood in predicting population quantities. Many models have not been adequately tested for their ability to predict existing or future wildlife and fish resources. Recently, increases in research into ecosystem structure and function, and community structure and function, may lead to improved techniques for predicting wildlife and fish resources.

INTRODUCTION

Periodic national assessments of renewable natural resources are required by the Forest and Rangeland Renewable Resources Planning Act of 1974 (RPA)[3] as amended by the National Forest Management Act of 1976 (NFMA).[4] The Soil and Water Resources Conservation Act of 1977 (RCA)[5] requires appraisals of the soil, water, and related resources. The Federal Land Policy and Management Act of 1976 (FLPMA)[6] requires inventories and documentation for development of policies and management of the nation's federal lands. Assessments are to be an integral part of land management planning and natural resource management processes within the United States Department of Agriculture Forest Service, National Forest System. These processes are guided by regulations which state that "Fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired nonnative vertebrate species in the planning area."[7]

The assessments and appraisals of fish and wildlife, mandated by the various laws and regulations require an analysis of present and anticipated uses, demand for and supply of the multiple renewable resources, and price relationship trends into the future. They also require an evaluation of various opportunities (e.g., application of alternative management prescriptions) for improving the yield of tangible and intangible goods and services from these multiple resources, together with estimates of investment costs and direct and indirect returns to the federal government.

Although the past 50 years of wildlife and fish management have involved decreasing emphasis on a

[3] *Public Law 93-378. United States Statutes at Large. Volume 88, p. 476 (P. L. No. 93-378, 88 Stat. 476).*

[4] *P. L. No. 94-588, 90 Stat. 2949.*

[5] *P. L. No. 95-192, 91 Stat. 1407.*

[6] *P. L. No. 94-579, 90 Stat. 2743.*

[7] *Federal Register. Volume 47, p. 43048 [47 Fed. Reg. 43048 (1982)] [Section of the Code of Federal Regulations affected is Title 36, Part 219.19 (36 C.F.R. 219.19)]*

description of the resources and an increasing emphasis on cause and effect predictions of change, wildlife and fish management has been slow to use new resource planning processes. Because wildlife and fish resources typically are not priced commodities, they may be considered external to the commodity planning process and treated as legally or socially imposed constraints (e.g., protection of threatened and endangered species). However, techniques that have been an integral part of the planning process in business and industry, such as trade-off analysis and optimization, are now being tested and required in renewable resource planning conducted by government agencies. This will help agency planners to better anticipate future capabilities and uses of natural renewable resources and to determine allocations of land, labor, and capital. It will also speed decisionmaking and provide improved planning techniques to reduce resource deficiencies and conflicts.

Before managers can effectively use these new techniques, however, current ecological knowledge and methods must be integrated with socioeconomic considerations in the decisionmaking process. This means developing an estimate of the quality and quantity of the resources in the nation's ecosystems over time. It also means developing an understanding of both the economic efficiency and social value of achieving this quality and quantity of the resources. Then the ecological, economic, and social considerations should be integrated to predict probable ecological, economic, and social outcomes under various assumptions about future supply and demand.

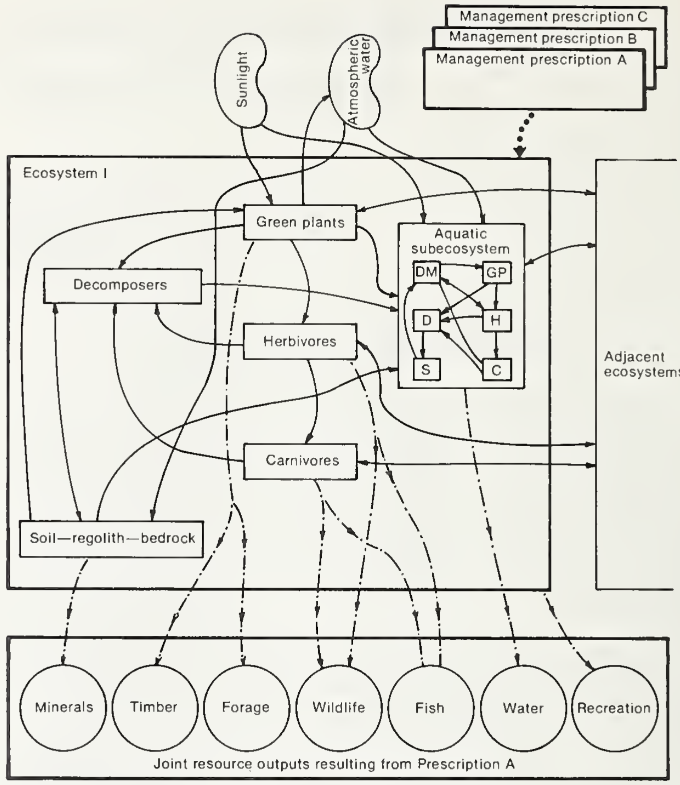

Figure 1.—Depiction of an ecosystem indicating the administration of one alternative management prescription and that a unique set of joint resource outputs result. ····> application of management prescriptions to ecosystems, ———> energy and material (elements) flows resulting from ecological processes, -·-·> energy and material (elements) flows resulting from harvest by humans, and recreation use other than harvest of wildlife and fish, DM -dissolved material, D - decomposers, GP - greenplants, H - herbivores, S - substrate, C - carnivores.

RESOURCE PRODUCTS COMPARED WITH ECOSYSTEM COMPONENTS

In a socioeconomic context, resource products are identified, named (e.g., timber, wildlife and fish, water, range), and incorporated into analytical procedures in terms of their perceived importance to humans. Many of the available analytical procedures reviewed in this paper were developed within this socioeconomic context and, in addition, were designed to answer single resource questions. Because such questions are about parts of ecosystems, answers require ecological analyses. However, because these questions are framed in a single resource, socioeconomic context, rather than in an ecosystem context, they deal only with small fractions of ecosystems. These parts usually are not equivalent to the ecosystem components used by ecologists (e.g., primary producers, herbivores, carnivores, decomposers; fig. 1) and are not usually organized in an ecosystem component/process framework (e.g., do not deal directly with energy flow).

Resource assessments that involve multiresource ecosystem components or processes must be designed to (1) predict the simultaneous response of all renewable resources (e.g., wildlife and fish, timber, water, range) to a present or future situation of an ecosystem, and (2) deal with conservation and protection of resources in order to maintain a sustained, optimum yield of all resources. Such analyses must deal with the stability, resilience, and cycles of ecosystem components/processes. Answers that are developed from within an ecosystem component/process framework must be converted into the terms of socioeconomic resource products (fig. 1).

GENERAL CHARACTERISTICS AND CRITERIA FOR EVALUATION

There are relatively few types of analytical techniques used in estimating the fish and wildlife resources. It is the particular combination of parts, the unique structure, the input variables used, and the degree to which predictions are made over time and at different spatial scales which distinguish the various techniques within a given type of output.

The techniques reviewed here have various limitations. In some cases, the knowledge of ecological requirements is lacking, but there are mathematical procedures for estimating the relationships. In other cases, the ecological relationships are well understood, but the mathematics have not been developed to ade-

quately express those relationships. In still other cases, knowledge of both the ecological and mathematical relationships is inadequate. Finally, the limitation may be in the existing techniques for collecting the needed data. In these cases, researchers must either develop better ways to measure the variables presently in use, or identify and test new integrator or surrogate variables for which data can be obtained more easily.

Ecological Analysis Techniques

Use of expert opinion is the most basic analytical technique. In this technique, an expert applies his or her knowledge of species-habitat relationships; species-habitat requirement variables; and population quantity, structure, and dynamics variables; to make estimates of wildlife and fish resources.

Some procedures utilize various standard multivariate analyses, such as principal components analysis, discriminant analysis, factor analysis, and cluster analysis.

Habitat quality analysis techniques involve a series of graphs, each with a curve relating quantitative levels of one habitat variable to the optimum for a given species. Each variable is represented in an equation in such a way as to reflect its importance relative to the other variables in the equation. Based on real or proposed situations, numbers (from 0 to 1) were taken from the graphs and placed in the respective expressions of the equation. Solution of the equation provides a number that is the index of habitat quality for a particular species in question.

The technique of pattern recognition analysis, coupled with Bayesian statistics, was first developed in diagnostic medicine. It is a procedure by which a specified group of variables, each with a specified range of values, constitutes a pattern for recognizing that a certain quality and quantity of habitat exists for a species. A certain population quantity of a species can be estimated if the relationship between certain combinations of habitat quality and quantity and population quantities has been determined.

Linear programing is an optimization technique which enables identification of the group of management practices, the intensity or level at which those practices must be applied, and the sequence in which they must be applied to achieve a selected wildlife or fish management goal (Davis 1967).

Depending on the model used, population dynamics models enable the investigator to predict population quantities, structure, and dynamics and harvest or yield. Again, depending on the model, single species and interspecies competitive interactions, predator-prey interactions, and fishing pressure also can be estimated. Mathematical procedures used in the models include differential and integral calculus, difference equations, matrix algebra, and life tables. Input data include population quantities, mortality, natality, and population sex, age, and/or size structure.

Another technique is the use of systems ecology models. These models utilize notation, such as that of Forrester (1961, 1968), and involve system sources, components, sinks, material or energy flows, information flows, and control gates. The models are designed to simulate the behavior of a small subsystem of an ecosystem or an entire ecosystem from which predictions of the wildlife and fish resource can be made.

Criteria for Evaluating the Ecological Analysis Techniques

The analysis techniques presented in this report are evaluated in terms of the attributes of the input data used and output data produced. The accuracy of most of the predictive techniques is not discussed in this report because there are no established standards by which to evaluate their accuracy. Most of the theoretical predictive formulas have not yet been tested. However, the paper includes a discussion of the factors related to the use and applicability of each technique in the assessment process.

Evaluation criteria considered include features of the input and output data, the subjectivity of the technique in using that input data to derive an output, and the degree to which the technique might fit into an integrated, multiresource analysis procedure. A completely integrated approach would include ecological analyses for estimating outputs of all the natural renewable resources simultaneously, analyses of economic costs and social benefits, and analyses that deal with all spatial hierarchical levels. When integrated procedures are discussed here, only natural, multiple resource, ecological analyses are considered.

Output Evaluation Criteria

1. Degree of information provided by the output:
   a. Habitat quality (suitability).—The potential of a given habitat to support a selected wildlife or fish species (usually expressed as a numerical value or index),
   b. Species occurrence.—The presence or absence of a selected species of wildlife or fish,
   c. Population quantities.—The total number or biomass of a selected species per unit of area (includes estimates of either the total population or the portion of the population that can be harvested according to some criteria), and
   d. Population structure and dynamics.—The sex ratio, age classes, size classes, and mortality and natality rates of a selected species population;
2. Time period over which the technique is applicable; and
3. Geographic scale to which the technique applies.

Input Evaluation Criteria

1. Quantity and quality of information supplied by the inputs:
   a. Species-habitat requirements variables,

b. Population quantity variables, and
c. Population structure and dynamics variables; and

2. Availability and objectivity of data:
   a. Number of variables,
   b. Variables estimated by expert opinion (expert opinion may provide high-quality data),
   c. Variables obtained by remote sensing,
   d. Variables obtained by field inventory, and
   e. Integrator variables used.

Incorporation of Effects of Management

Except in the techniques that estimate harvest population quantities, management practices, as such, do not enter into the procedures. However, management practices cause changes in one or more of the habitat requirement input variables. Some practices affect populations directly. Therefore, in order to predict the effects of management practices, it is necessary for the analyst to identify the variables affected, and to quantify the amount that a practice would change these variables. This relationship is rarely described in the literature.

A DESCRIPTION AND EVALUATION OF THE ECOLOGICAL ANALYSIS TECHNIQUES

TERRESTRIAL WILDLIFE ANALYSIS TECHNIQUES

The ecological analysis techniques needed to estimate terrestrial wildlife resources in a land management planning context have developed towards three interrelated goals. These are estimation of habitat capability, species occurrence, and population quantity and structure. Some techniques incorporate aspects of all three goals. However, most can be classified into one of these analytical types.

Habitat capability techniques generally develop an index based on an inventory of habitat variables related to the habitat requirements of wildlife species. A species is assumed to occur in habitats that are determined capable of meeting the species requirements. These techniques have found general acceptance for use in mitigation type evaluations.

Species occurrence techniques incorporate known information on species occurrence with an inventory of species habitat variables to develop prediction equations. These equations assume that when habitat conditions are found within the range of those evaluated in developing the model that the species will be present. Tests of this assumption are important but are infrequently carried out. The use of species occurrence techniques in large land area analyses largely depends upon the availability of occurrence or population density data; the latter is more desirable.

The requirements of techniques for predicting wildlife population quantities and structure are the most difficult to meet of those discussed. These techniques incorporate habitat and species population inventories to develop statistical models. They also include habitat requirements to develop simulation models. The major difficulty in developing and using these techniques is the deficiency in population data. As a consequence, this technique frequently is used to calculate potential populations without the necessary estimates of error.

Habitat Estimation

Habitat has long been used as an output measure in wildlife production analyses, because it is easier to measure than animal populations. In nearly all of the analytical methods discussed here, habitat variables are used to determine a habitat rating; this rating is usually expressed as a quality or suitability index of the habitat's capability to produce wildlife. Early terrestrial wildlife techniques that predicted or calculated habitat quality generally tended to be characterized by subjectivity. As the procedures developed, more emphasis was placed on quantitative methods. The techniques reviewed tended to analyze local, current conditions, and rarely appeared to be applicable at the regional scale of analysis. Analysis of future habitat conditions is possible when associated analytical methods are used to project the habitat variables into the future, and assuming that species habitat relationships remain constant.

Analysis techniques developed by Buckner and Perkins (1974), Hamor (1974),Hawes and Hudson (1976), Whitaker et al. (1976), and Boyce (1977) typify early efforts relying heavily on expert opinion in evaluating habitat suitability.

Buckner and Perkins (1974) attempt to establish a compromise between intensive documentation and visual estimation of wildlife habitat status on industrial forest land. The procedure involves a systematic sample of a timber tract that is stratified by forest stands. Each plot is visited and assigned a numerical rating from 1 (very poor habitat) to 6 (excellent habitat) for each species under consideration. The rating is based solely on the evaluator's knowledge of each wildlife species and his perception of potential limiting factors. An average habitat value index is then calculated for several sample sites within a forest stand. An index value for the entire tract is obtained by summing the weighted average of each stand value. Relative weights are based on the percentage of total acres represented by each stand. Because this method is subjective, no standard species-habitat relationships can be established, resulting in the potential for inconsistent evaluations. It is not possible to update the stand or tract indexes without a new field survey.

Hamor (1974) provides a similar methodology; however, the habitat suitability indexes represent wildlife in general. The technique was developed primarily to help mitigate effects of local water and related resource developments. Again, the quality values are obtained subjectively through the use of tables that: (1) first describe a small set of habitat conditions (e.g., evenaged hardwoods with an open understory and overgrazing by livestock) and, (2) assign a relative index value

ranging from 0-1 for each defined habitat condition. A composite habitat value is obtained by multiplying the relative index by the total acres under evaluation.

Expanding the scope of application to a regional scale, Hawes and Hudson (1976) proposed a method, based on a biophysical landscape classification, that uses an evaluation of each land system's capability to provide the required habitat for selected species. Areas are classified into land forms with associated climax vegetation and soils. The system converts classified inventory data into a suitability rating for a species. Information on species requirements comes from literature and expert opinion. Their method concerns only species that use climax vegetation. The final output is a qualitative habitat suitability rating.

Whitaker et al. (1976) developed models, for species characteristic of the Maryland Piedmont region, that use line charts to establish species-habitat relationships. Each line chart represents a linear scale used to inventory habitat characteristics such as average tree diameter at breast height, percent ground cover of understory, percent herbaceous ground cover, etc. The line charts for each habitat characteristic are translated into a suitability index using a transformation scale that is species specific. A weighted average for an entire habitat type represents the final output.

The DYNAST (Dynamically Analytic Silvicultural Technique) system developed by Boyce (1977) is an attempt to analyze multiple benefits. The habitat evaluation submodels are based on easily inventoried habitat variables (e.g., the distribution of size class and forest openings) which represent the more numerous and complex species-habitat relationships identified for each species. A curvilinear relationship is established for each variable, which relates possible variable values to a habitat index. A mathematical algorithm defined by the model builders is then used to combine the individual variables into a single habitat index.

A more recent implementation of the professional judgment technique in a multiple use context is the Information Management on a Grid Cell System (IMGRID). This system (Davis 1980) enables consideration of wildlife habitat suitability. Calculation of the habitat rating involves species-habitat relationships (as determined by biologists) and seasonal variation in habitat requirements; a weighting procedure is used to express the relative importance of the habitat components. The actual input variables depend on the species under consideration; however, the broad categories examined include food, water, cover, reproductive requirements, special requirements, and interspersion. The mathematical manipulation function of IMGRID is used to sum values to arrive at a composite habitat rating. The evaluation delineates relatively homogeneous areas each of which has specific capabilities to provide the requirements of a particular species.

In an attempt to alleviate the lack of concurrence among subjective evaluators, Thomas et al. (1976) developed extensive guidelines for evaluating habitat quality. The concept they used in developing the guidelines came from Haapanen (1965). Outputs from these guidelines are wildlife species richness, plant species richness, diversity, and stability. The guidelines were based on several assumptions:

1. Wildlife production is generally a by-product of management for other resources.
2. The ability to predict wildlife population quantities, over time, is the weakest link in an assessment.
3. Lack of knowledge is less of a problem than lack of a conceptual framework for:
   a. consideration of all terrestrial vertebrates,
   b. retention of the ability to emphasize a particular species, and
   c. identification of specific habitats requiring special attention.

The guidelines developed by Thomas et al. (1976) represent a set of relationships between habitat variables and species response. The response, however, is not equivalent to predictions of habitat quality, species occurrence, population quantities, sex structure, or age structure. There are three parts to the guidelines:

1. The relationship of all vertebrates to forest communities and successional stages (four levels of information are provided):
   a. response of all vertebrates, condensed into 16 life forms, to community and successional stage of the habitat;
   b. response of individual species within the life form;
   c. detailed biological data on each species; and
   d. guidance to additional literature on each species.
2. Guidance on methods to give special consideration to a particular species.
3. Consideration of special and unique habitats or habitat components.

Information obtained using these guidelines is then used in the planning process to affect the management of other resources.

This approach allows wildlife managers to make specific statements regarding which species, or groups of species, will be affected by management prescriptions applied to the habitat. Based on this, recommendations can be made through the land management planning process to minimize adverse impacts on wildlife habitats through management activities.

Another approach is to base the suitability index on objectively derived measures. Methods described by Brabander and Barclay (1977) and Asherin et al.(1979) both rely on habitat diversity to arrive at habitat quality ratings.

Brabander and Barclay (1977) utilized LANDSAT digital imagery data to establish wildlife habitat quality ratings for north central Oklahoma. The results of cover type classification of LANDSAT data is used to compute a vegetative cover diversity index. All plots are stratified based on these vegetative cover diversity indexes. Faunal and plant species data are then collected and used to calculate faunal species diversity and plant species diversity indexes. The three diversity measures are then subjected to correlation analysis to test the validity of using LANDSAT generated cover diversity measures as an indication of wildlife diversity. Signifi-

cant results were obtained (Brabander and Barclay 1977) lending credence to this method of evaluating habitat for wildlife as a whole.

Asherin et al. (1979) developed a similar remote sensing methodology based on the assumption that habitat quality is a direct function of habitat diversity for most terrestrial vertebrates. This method uses a stepwise multiple regression model to calculate habitat quality from habitat diversity measures computed from color infra-red aerial photographs. The most efficient predictor of habitat quality was a model containing bird species diversity as the dependent variable and with habitat strata diversity and habitat cover type diversity as independent variables. Although the prototype was developed in southeastern Montana, the procedure should have generic application, provided data are available to establish the regression models.

Federal agencies have put considerable effort into developing habitat evaluation procedures to meet their specific needs. Most of the following involve specific combinations and refinements of the approaches discussed previously.

In 1980, the U.S. Army Corps of Engineers reported on the development of a Habitat Evaluation System (HES) for planning purposes. The Habitat Evaluation System is based on a series of graphical relationships between key variables (e.g., percent overstory, number of snags, percent understory) for major habitat types and suitability indexes for those key variables representing their suitability for wildlife. The relationships are determined from literature sources and expert opinion. The Habitat Evaluation System describes habitat quality for a broad range of species rather than for individuals or groups of species. The output is a composite habitat suitability index ranging from 0 to 1 for each major habitat type. The relationships used in the Habitat Evaluation System are based on conditions in the Lower Mississippi Valley where the system was developed. Consequently, application in other areas requires modifications.

The U.S. Fish and Wildlife Service developed Habitat Evaluation Procedures (HEP) (U.S. Department of the Interior, Fish and Wildlife Service 1980, 1981; Schamberger et al. 1982) for use in evaluation of project impacts. The method is based on a species-habitat relationship that assumes optimal habitat for a species can be defined and that comparisons can be made between actual on-site conditions and the optimum. The Habitat Evaluation Procedures establishes a habitat suitability index value for a given species and combines the index value with an area measurement to give a habitat suitability per unit of area index as a final output. The method assumes that this unit value is directly related to carrying capacity. Like HES, the species-habitat relationship used in Habitat Evaluation Procedures are location specific. Such location specific applications are also found in Flood et al. (1977) and Baskett et al. (1980).

The Fish and Wildlife Habitat Relationships Program of the USDA Forest Service was developed for use in land management planning on National Forests (Nelson and Salwasser 1982). The method is based on labeling habitats according to dominant biological and/or physical attributes of sites and the specific environmental variables that are habitat resources for certain species. Three levels of detail for the biological and physical attributes of a site are evaluated in terms of diversity and selected species habitat capability for application in project and land use plans. Level 1 models develop habitat capability ratings for high, moderate and low densities of species. Known population densities are required to calibrate the habitat capability ratings. Level 2 models are frequently those developed by others (e.g., U.S. Department of the Interior, Fish and Wildlife Service 1980, 1981; Schamberger et al. 1982; and Williams et al. 1977). These models are assumed to integrate habitat variables and rate these variables in terms of providing habitat requirements. Level 3 models serve the purpose of aggregating all habitats within one area such as a National Forest. The approach developed by Thomas (USDA 1979) is one of several used for Level 3 models.

The Soil Conservation Service (SCS) evaluated changes in habitat quality as part of their 1980 Soil and Water Resources Conservation Act Appraisal, Part II. This effort was national in scope. Using existing inventory data, SCS established quality ratings by land use. A habitat quality index based on a scale of 0 to 1 is calculated for primary land uses (e.g., cropland, rangeland and forest land). Vegetation characteristics from the inventory are selected as being important indicators of habitat quality and assigned values. The quality ratings are determined by adding the weighted values of all variables for a given land use and dividing by the total of all weighted values. The indexes show only relative differences in habitat quality. This system does not measure suitability of the habitat for any one species and is subjective. Evaluation of projected changes in land use practices that would affect the habitat are made, permitting quality ratings for future conditions.

A property that characterizes most of the procedures discussed is that they have been developed and applied on a local scale. However, systems developed by Whitaker et al. (1976), Brabander and Barclay (1977), Asherin et al. (1979), and Hawes and Hudson (1976) do have regional application. Similarly, the HEP system (U.S. Department of the Interior, Fish and Wildlife Service 1980, 1981; Schamberger et al. 1982) has potential for evaluating habitat at the local and regional scales.

Analytical procedures that use species-habitat relationships can predict future habitat quality by analyzing changes in habitat structure variables projected by other models. The techniques discussed to this point do not provide a satisfactory connection between the measured attributes of habitat suitability and carrying capacity. In most cases, this association remains to be developed and tested. HES (U.S. Army Corps of Engineers 1980), HEP (U.S. Department of the Interior, Fish and Wildlife Service 1980, 1981; Schamberger et al. 1982), Forest Service Species Habitat Relationships (Nelson and Salwasser 1982), and systems developed by Brabander and Barclay (1977), Asherin et al.(1979), and Whitaker et al. (1976) assume that species habitat relationships are constant in predictions of future habitat

quality or suitability. As a rule, habitat quality cannot be expressed for wildlife communities, because as habitat variables change, habitat quality is reduced for some species and improved for others.

Species Occurrence Estimation

Techniques used to estimate species occurrence relate a set of habitat variables that are relatively easy to inventory to a species occurrence variable that is more difficult or expensive to obtain. Based on known relationships between these variables, models are developed and tested. The models are then used to predict species occurrence, provided that habitat variables can be inventoried which are the same type as are in the model, and their values are in the range of those used in building and testing the model.

Hoar (1980) attempts to predict the distribution of several endangered mammals in Virginia by using a system based on the distribution of environmental factors associated with the historical ranges of the species. The environmental factors are identified by a literature review and are classified as requisite factors or enhancement factors. Geomorphologic, topographic, land use, and physiographic data are included as input variables into the species historical range prediction. Computer analysis is used to synthesize habitat data and to describe probable distribution over large areas. One important shortcoming, however, is the fact that no probabilities are assigned to the prediction. Although variation in the suitability of a particular habitat to a particular species is accounted for, there is no method for determining the model's validity in terms of predicting the probability of occurrence.

Williams et al. (1977) developed a technique that associated probabilities with an estimate of occurrence. They adapted pattern recognition techniques from diagnostic medicine and coupled them with Bayesian statistics to evaluate wildlife habitat; their system is called PATREC. Kling (1980) was the first to field test the PATREC approach, and determined that it can be used to predict species occurrence. Kling (1980) developed such an occurrence model for golden eagles in the northern great plains region (southeastern Montana and northeastern Wyoming). Included in the model are variables that address both abiotic (e.g., presence of cliffs, snags, remote location) and biotic (e.g., prey density, shrub density, distance to other active nests) factors. Specific input variables are designated through literature reviews, expert opinion, or empirical field research. However, when based on other than empirical research, this method suffers from subjectivity. Minimizing the subjective component of this technique would appear to strengthen its reliability in estimating species occurrence.

Within the last decade there has been considerable development in the application of multivariate statistical methods in analyzing wildlife habitat. Shugart (1981) summarizes some reasons for this development:

1. Multivariate procedures intrinsically fit ecological problems (and data) dealing with habitat selection.
2. Many of the multivariate methods seem to be robust in the face of mild deviations from the underlying assumptions.
3. There already exists a hypergeometric interpretation of relationships among animals (niche theory) that is essentially based on a multivariate sample space.

Although multivariate techniques usually have habitat suitability as the output, the actual methods of determining species-habitat relationships and model validation make these methods more appropriately classified as estimates of species occurrence. Model building procedures involve comparing habitat characteristics of areas occupied and unoccupied by a particular species. For a review of possible input variables see Anderson (1980). Model output is usually expressed in terms of suitable or unsuitable habitat which is readily translated into "areas that should support" or "areas that should not support" the species of interest. The models developed by Smith et al. (1981) using discriminant function analysis provide an example of applying multivariate methods in predicting and simulating over time the availability of suitable habitat (i.e., percent area that should be occupied) for a number of eastern Tennessee birds. Input variables in the models include measures of foliage, branch, and bole biomass of trees, and stem density. Other applications of multivariate methodologies were reviewed in a workshop on the use of these statistical techniques in wildlife habitat studies (Capen 1981).

Estimation of species occurrence is an important contribution to interpreting species habitat relationships beyond the calculation of habitat capability or suitability indexes. The recent use of statistical techniques in the PATREC and multivariate approaches has greatly improved the value and interpretation of species occurrence models. As is generally true, most of the models need to be validated and field tested. Statistical methods are valid when assumptions concerning data used in these methods are adhered to carefully.

Population Quantities and Structure Estimation

Terrestrial wildlife population quantities could be predicted, in part, by incorporating components of the techniques discussed previously with information on population demography. However, demographic data on wildlife species is extremely difficult to obtain. Primarily for that reason, very few techniques produce accurate and precise information. Many species of wildlife do not lend themselves to direct estimation of mortality, fecundity, or population structure, because their mobility, behavior, or other characteristics make inventory of these variables difficult. In many cases, the techniques discussed predict potential rather than actual population quantities and tend to be characterized by subjectivity. Professional judgment is required to make the conversion from habitat to population numbers.

Early efforts to use demographic variables in models of population growth are simplistic; however, they

define the theoretical foundation for the more current, complex simulations.

Another class of techniques uses both habitat and demographic variables in a simulation model. These techniques tend to require intensive inventory data and have not been rigorously tested. The scale of application in most cases is for local situations. However, several techniques appear to be applicable at the regional level, and several others may be able to be modified for use at the regional level.

The problems associated with indexes of habitat value for wildlife and fish species which are used in resource planning are that these relative indexes are meaningless unless the functional relationships and actual population quantities can be determined. Three broad approaches attempt to establish measures of wildlife quantities and population structure.

Lentz (1973) described a system that epitomized the early species-habitat relationship approach. The technique translates a habitat quality rating into potential populations of four game species in the Alabama River Basin. In this system, species-habitat relationships are defined by a review of the wildlife research literature, and various habitat variables are inventoried to establish a habitat rating. The variables inventoried are species specific and include: overstory, midstory, and understory condition; percentage of cover types; presence of breeding and feeding habitat; stand age; interspersion; and years since last burn. Once the habitat rating is determined, a field biologist assigns a potential carrying capacity to the habitat rating. Carrying capacity values for each habitat rating are multiplied by acres in each habitat condition to derive a potential population. The derivation of this population value is based on the assumption that the species already occurs in the area or that it can be introduced.

Willis (1975) developed a nearly identical technique for several game species found in Kentucky. His method is based on described species-habitat relationships and measurement of habitat variables to arrive at a qualitative rating of habitat condition. A potential carrying capacity estimate is assigned to each habitat condition by field biologists or by reviewing past research reports. The primary difference between this technique and Lentz's (1973) is that the habitat variables inventoried by Willis are more definitive and do not require the subjective judgment of the evaluator in rating habitat condition.

Efforts to reduce the subjectivity inherent in systems dependent upon the literature or human judgment have resulted in several techniques that either establish species-habitat relationships empirically or determine the qualitative function relating the suitability index to abundance. The PATREC system reviewed earlier is also applicable to estimations of wildlife population numbers. This technique establishes the species-habitat relationships by associating particular habitat characteristics with relative population classes (e.g., high or low population levels) using a frequency of occurrence analysis. These frequencies of occurrence are translated into probability statements that can be used to analyze areas of unknown potential for supporting a particular species. The output of this intermediate step is a group of probabilities that quantify the ability of the area to support the defined relative population classes. These probabilities then can be used to estimate a potential carrying capacity by incorporating historical population inventory data, which are used to calculate an average population level for each relative population class. The carrying capacity for the entire area is computed by summing the products of the average inventory estimates and their respective probability statements.

Lines and Perry (1978) attempt to establish the relationship between an index of habitat quality and wildlife abundance using correlation and regression analysis. The habitat quality index is determined with the following model:

$$HI = \frac{\sum_{n=1}^{3} (A_n)(X_{1,n})(X_{2,n})(X_{3,n})}{A_T}$$

where: HI = wildlife habitat quality index

n = subscript of the vegetation type (woodland, grain and seed crops, grasses and legumes)

A_n = total acres in vegetation type n

A_T = total acres in the plot

$X_{1,n}$ = interspersion index for vegetation type n

$X_{2,n}$ = factor accounting for the management characterizing each vegetation type n

$X_{3,n}$ = estimated value of the distribution of wildlife drinking water

Correlations between habitat indexes and individual avian species populations were insignificant. However, a pooling of population estimates across all species resulted in significant positive correlations. Regression analysis provided the prediction equations for both avian diversity (number of species) and avian density from a measure of habitat quality.

Willis (1975), Lentz (1973), and Lines and Perry (1978) developed systems that calculate a habitat quality rating as an intermediate output with the final output, population quantity, based on this habitat rating. Giles and Snyder (1970) outlined an earlier system that did not consider this intermediate step but calculated potential populations directly from various habitat variables. Giles and Snyder assumed that the major factor in determining potential big game population density is the amount of available forage in an area used by animals during the critical or stressful periods of the year. Based on this assumption, habitat factors, such as year of origin (in a successional sequence), successional stage, elevation, acreage, percent acreage in winter range, quality factor (which accounts for nutritional variations), and percent composition, are inventoried. The system is capable of predicting potential populations at some future time, if no major habitat changes occur during the period of simulation.

A more recent application of the concepts outlined by Giles and Snyder (1970) is found in Wallmo et al. (1977), who developed a technique that evaluates current habitat quality for mule deer in north central Colorado. The method is based on an inventory of energy and protein supplied by available forage. A simple ratio between energy and protein required by the species and energy and protein provided by the habitat results in a prediction of potential carrying capacity. Existing data on the nutritional requirements of mule deer are sufficient to allow such an evaluation. However, nutritional and energy requirements are unknown for most species of wildlife.

Recent advances in multivariate analysis also have applications in predicting wildlife abundance based on habitat characteristics. Kitchings and Klopatek (1982) developed a regional level methodology using discriminant function analysis, for a few species representative of the western, central, and eastern United States. The models utilize acreages of Kuchler (1964) vegetation types and land-use categories as macro-scale input variables. The output is always in the same units as the input. In most cases, the units of input and output are a measure of abundance; however, in two cases, relative population levels (i.e., absent, low to moderate levels, high to very high) and animals killed on the road are used as surrogates. Although preliminary reports are positive, the models have not been validated.

A second group of techniques that estimate population quantities involves those methods that focus primarily on demographic input variables. Some of the earlier methods had several deficiencies. The most significant shortcoming was that many of the techniques offered only theoretical insight into the ecological processes involved in population dynamics. For example, the methods proposed by Gause (1934), Lotka (1924), and Volterra (1926) were developed to simulate predator-prey interactions and competition. However, their objective was not to predict animal population levels but to gain a basic understanding of the ecological processes involved in an environment where animal populations were competing for limited resources. The assumptions made to simplify the system, therefore, severely limited application to the real world. Another deficiency of Gause's, Lotka's, and Volterra's work was their failure to incorporate age structure into the model design. Despite the lack of realism and the simplicity of these systems, these early efforts provided the fundamental concepts and knowledge upon which many of the more modern and sophisticated models are based.

In response to the deficiencies of earlier methods, Leslie (1945) developed a matrix algebra model to account for the observed differences in birth and death rates associated with age. The population is differentiated into age groups, and the appropriate birth and death rates are assigned to each group. This modification increases the realism of population models to the point where later investigators have shown that abundance and population structure projections agree well with short-term experimental data for a number of wildlife species (Fowler and Smith 1972). Because it has functioned effectively for a number of populations, this method has been incorporated into more recent models.

Pennycuick et al. (1968) made some additional modifications by incorporating both competition and time lag factors in the modeling effort. He modified Leslie's approach by making fecundity and survival density-dependent, and by introducing time lags. This model has shown some theoretical validity in predicting structure but has not been validated with empirical data.

Caswell (1972) and Comins and Blatt (1974) also identified certain weaknesses in the formulations of Volterra and Gause. Caswell proposed inclusion of factors to account for time lags, prey refuges, and "hunger" of the predator population. Comins and Blatt suggested a term to simulate the effects of environmental heterogeneity on population dynamics. Although the objectives of these models were not directed at predicting actual population levels, they identified factors that may be important in understanding the dynamics of population growth.

Methods to predict population structure in terms of age and sex for terrestrial wildlife, such as the Leslie (1945) method, are rare. The most common method of predicting population structure in wildlife management evolved from life table analyses. In this technique, population simulation focuses on the input variables of initial population structure and mortality rates specific to a species. Outputs from traditional life table analysis include mortality or survivorship schedules in a particular population. Widespread application has been limited because of the nature of the data requirements. Information on the initial age and sex structure must be estimated in order to predict population structure. However, as was stated earlier, such inventory data on wildlife species may be difficult to obtain and can be costly. The basic deficiencies in such an approach have been identified by Eberhardt (1969):

1. Life tables tend to ignore reproductive rates by considering only losses.
2. Life tables apply only to a population at a given point in time or to "stationary" populations, where it is assumed that births exactly balance deaths and that all rates are constant over the history of the population.

If the actual dynamics of a population are to be understood adequately, modifications to the "classic" life table approach are needed. To help resource managers evaluate a population's response to a certain set of circumstances induced by management or inherent in the ecosystem, Caughley (1977) found that both mortality and fecundity schedules must be considered. This approach was used in modeling both the statewide bobcat population for Wyoming (Crowe 1975) and a resident flock of Canada geese (Cromer 1978). Again, both reproduction and mortality factors, according to age class, were considered. Crowe used regression techniques to adjust his age-specific survivorship. Cromer used the simulation model PROGRAM ONEPOP developed by Gross et al. (1973) to describe his population, which also made use of harvest rates as a more specific breakdown of mortality.

PROGRAM ONEPOP was designed primarily for use on big game herds; however, application appears to be more generic, based on Cromer's usage on Canada geese. Data requirements include information on reproductive and mortality rates, age and sex structure, harvest rate, differential age kill, hunting effort, wounding loss, minimum age to harvest, minimum age to bias sex kill, and functional equations relating (1) density to production and energy used, and (2) age to weight and antler growth. Output from simulation runs concern population size, number of animals harvested, quality of animals harvested, weight of animals harvested, and energy required to produce yield. Preliminary tests of validity show good alignment between predicted and observed population levels for short-term simulations. Consequently, simulations for greater than 10 years may require modification of the functional relationships inherent in the model (e.g., modification of the equation for density dependent reproduction rates).

One of the most extensive applications of the life table approach through computer simulation was conducted by Craighead et al. (1974) on the Yellowstone grizzly bear population. The model was developed from long-term data and is capable of projecting future population levels. Consideration of age and sex allowed for management recommendations and prediction of possible effects resulting from various harvest or habitat management actions. The biological variables discussed above are included in the model structure along with the external effects of hunting and other management actions. Future projections are based on the assumption that reproductive rates would remain unchanged.

From the previous discussion of predictive techniques describing population quantities, two major categories of procedures can be identified:

1. Those that base their population predictions (usually for potential populations) on habitat factors.
2. Those that base their population predictions on population structure and dynamics (usually from inventories of actual populations).

From an ecological view, it is necessary to combine the two kinds of techniques in order to get a more accurate estimate of either potential or actual population levels. A system utilizing both types of information would also be useful in estimating the rates of increase or decrease of a particular population related to management prescriptions implemented within an ecosystem.

Davis (1967) was one of the earliest researchers to include both habitat and demographic variables in a single analysis for white-tailed deer. Dynamic linear programming was used to simulate deer populations over time. Input variables included: mortality, fertility, browse production, browse consumption, breeding requirements, and a mathematical expression representing the management objectives. This model provides insight into long-term yield, harvest schedules, and various management practices to maintain the deer herd. The technique also can be modified to incorporate multiple resource considerations. The most limiting aspect of this approach is that it assumes that all ecological relationships can be represented with a linear equation.

Rykiel and Kuenzel (1971) introduced nonlinear equations into a simulation model, in their study of the Isle Royal wolf community. By incorporating plant production, energy supplied by plants, respiration rates of plants as habitat variables; wolf population numbers, prey (moose) population numbers, and mortality rates as demographic considerations, Rykiel and Kuenzel found increased realism with nonlinear equations. The output from the model is expressed in forms of steady-state standing crop quantities for both predator and prey species. Powell (1979) applied these concepts in an investigation of the fisher/porcupine/snowshoe hare community in the Upper Peninsula of Michigan.

Multivariate statistical methodologies are also proving to be useful in efforts to model animal communities. Poole (1971) utilized factor analysis to model the populations of 10 species of insects. This technique specifies the predictive equations and identifies the underlying factors causing variance in population levels. Consequently, only those variables shown to have a significant effect on the output are included in the models. Variables in the analysis included interaction coefficients between each species along with gross environmental factors (i.e., minimum temperature, maximum temperature, and rainfall). Simulations over time agreed well with actual values for common species. One drawback of this approach is that it requires tremendous amounts of field work to inventory the population. This problem is characteristic of most simulation models and represents one of the tradeoffs when increased realism is desired.

Garcia et al. (1976) attempted to incorporate both habitat variables and population structure and dynamics variables into one model for a black-tailed deer population of western Washington. The demographic variables are essentially those used in Leslie's matrices. Basically, the methodology involves a "projection matrix" that represents the fecundity and survival rates for each age class. A population vector defining the initial structure is multiplied by the "projection matrix" to produce the new population structure, one time unit in the future. Demographic components are integrated with the habitat elements by simulating the relationships between habitat variables and density dependent population variables, such as fecundity and mortality. Distribution of seral stages, percent canopy closure, snowfall, and succession are some of the habitat factors used. Although the methodology and concepts applied in the modeling effort may be applicable to different and larger geographical areas, the model has yet to be validated, even on the area for which it was developed.

The model developed by Medin and Anderson (1979) represents one of the most intensive efforts at incorporating habitat, population structure, and dynamics variables in a model to simulate a population of mule deer in Colorado. They also considered environmental factors in order to link the population to its habitat. Habitat factors, such as percent ground cover, percent vegetational composition, food yield, food utilization, weather, soil moisture, and snow depth, were inventoried. Population input variables included age structure, sex structure, mortality, birth rates, and harvest

rates. The resulting model allows prediction of future population densities and structure, and examination of the effects of various harvest strategies. The concept of feedback loops was paramount in the establishment of this system. Feedback loops have been used extensively in describing physiological systems, and are now receiving more consideration in wildlife studies. Medin and Anderson's (1979) system can quantify changes in variables over time and allow more accurate projections into the future. The authors also discuss species interactions in terms of competition and predator-prey relationships but make no further mention of these factors when describing the input variables in the model. This model requires much data and demands very specific knowledge of the population biology of a species as well as the species-habitat relationships. Where sufficient data exist, such a technique could be very useful. Unfortunately, the necessary data for such models is generally lacking.

The quantities and structures of terrestrial wildlife populations can be estimated from either or both habitat and demographic variables. The analytical capability has been developed for quite sophisticated analyses, although the ecological theory supporting these approaches has not been generally agreed upon. Data, particularly for demographic variables, is deficient in terms of both availability and quality. These analytical approaches, however, are a valuable means of defining the most critical data needs.

Most of the recent population simulation models discussed, whether concerned with potential or actual population levels, have some provisions for predicting future population responses. However, certain assumptions are made that attach qualifications to the estimate. For example, the PATREC system (Williams et al.1977) calculated the long-term potential mean population density that a particular set of conditions would support. The word "potential" is used because current models have been developed only for analysis of relatively stable environmental conditions. Features that may vary widely from year to year are not taken into account. Presence of the species in an area is assumed in these procedures. The fact that such assumptions are rarely valid is an admitted deficiency.

Several investigators have taken variables that are frequently assumed to remain constant and varied them to simulate population responses over time. In most cases, the hypothetically manipulated variables are those affected by management practices. Both Crowe (1975) and Powell (1979), for example, varied mortality rates resulting from increases in harvest rates to predict probable responses in the population. In addition, Medin and Anderson (1979) simulated the more long-term effects of varying harvest strategies in terms of sex, age, and time. Crowe, Powell, and Medin and Anderson, however, varied the habitat condition in terms of forage production. Similarly, Rykiel and Kuenzel (1971) introduced perturbations into the plant component of their Isle Royle community model and measured the subsequent response in the moose and wolf component over a 12-year period.

These techniques are directed toward small scale situations. Research dealing with regional or national level population estimates and population responses is essentially nonexistent.

Three levels of analytical techniques for evaluating terrestrial wildlife in land management planning activities have been reviewed. Habitat capability or suitability indexes are the most easily implemented methods available. However, they offer no direct information about the species occurrence or demographic attributes that respond to land management actions. Species occurrence and demographic models that incorporate habitat variables in their estimation procedures potentially solve that problem in the habitat models. The species occurrence and demographic data limitations, along with the lack of an agreed upon body of ecological theory, limit the utility of simulation models. Multivariate statistical techniques currently provide the most valid and rigorous means to evaluate land management actions on terrestrial wildlife.

AQUATIC WILDLIFE AND FISH ANALYSIS TECHNIQUES

Ecological analysis of aquatic wildlife and fish resources is most highly developed in determining habitat quality and population quantities in lakes and ponds. Recent efforts have been made to improve analysis models for rivers and streams. No techniques are available to predict species occurrence in any aquatic habitat, and few predict population attributes such as sex ratios and numbers, age structure and numbers, or size structure and numbers. Only rarely do analysis techniques predict aquatic wildlife resources over time. Most of the techniques are empirical. Cause and effect relationships and the interactions of the various ecosystem components have not been modeled for many situations. Simulation of ecosystem behavior by modeling would allow greater predictive accuracy and precision. Most of the techniques are applicable only to the present resource conditions, on a local scale, for one species or population.

Habitat Estimation

Efforts to develop predictive capability for aquatic habitat have been restricted to determinations of habitat quality or suitability for a given species. These techniques input only abiotic factors; they do not include biotic factors, such as the presence of predators, competitors, or disease, and they do not incorporate habitat size. Accessibility of the habitat to known reservoirs of the species in question seems to be assumed in these techniques. The methods depend on assembly of the habitat factors believed to be important in determining habitat quality for a species or group of species. Some of the procedures incorporate mathematical expressions for the relative importance of the factors, but none incorporates a description of the functional behavior of species-habitat nor species group-habitat systems. Also, they do not predict changes in habitat over time but only make predictions for the current situation.

The U.S. Fish and Wildlife Service has developed habitat evaluation procedures for individual aquatic and terrestrial species (U.S. Department of the Interior, Fish and Wildlife Service 1980, 1981; Shamberger et al. 1982). Habitat quality of a site, for a particular species, is expressed as a habitat suitability index (HSI). Species habitat requirements are obtained from the literature. A species response to each habitat requirement or abiotic variable (such as temperature) is graphed as a suitability index (SI) ranging from 0 to 1 (fig. 2).

Each variable is represented in an equation in such a way as to reflect its importance, relative to the other variables. Given an actual or a proposed situation, SI values are read off the various variable-SI graphs and those values are put into the HSI equation. Solution of the equation provides the HSI for a particular species.

The U.S. Fish and Wildlife Service has also developed an incremental method for assessing the effects of streamflow regimes on riverine habitats (Bovee 1978, Grenny and Kraszewski 1981). Depth, velocity, substrate, and cover information for a particular stream or river reach are used to establish a "weighted area" available as habitat for the various life stages of an aquatic species.

A guilding procedure being developed primarily by Henry L. Short[8] identifies what he refers to as breeding and feeding niches in a series of vertical strata within a vegetation type. Where aquatic systems exist, strata within the water column are included. A two-dimensional matrix is constructed: strata with feeding niches within strata are plotted on one axis, and strata with breeding niches within strata are plotted on the other. Field observations of a species are used to define where, in the vertical strata, the species occurs when it is feeding and breeding. When several species are grouped on the matrix, they are said to be a guild. Common habitat requirements for the guild can be identified from the matrix. Cluster analysis is used to mathematically assist in grouping species into guilds. This procedure identifies habitat used by a guild of animal species and also may be used as the basis for evaluating habitat quality for a guild.

[8]*Short, Henry L., and Kenneth P. Burnham. A technology for structuring, evaluating and predicting impacts on wildlife communities. U.S. Fish and Wildlife Service, Western Energy and Land Use Team, Fort Collins, Colo. (unpublished manuscript).*

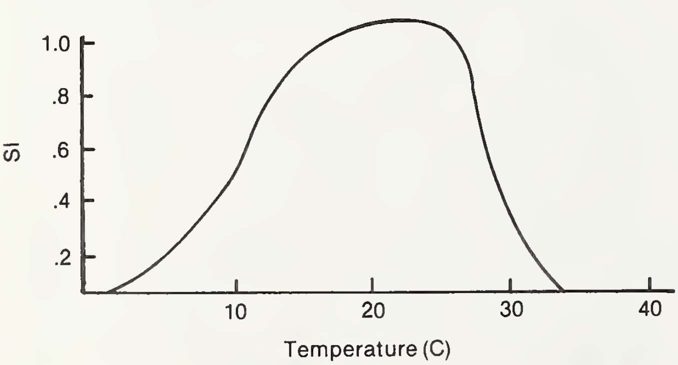

Figure 2.—Species response to the abiotic variable temperature, graphed as a suitability index (SI).

Swanston et al. (1977) developed an approach to predict habitat quality of streams for pink and chum salmon in southeastern Alaska. They tested 21 geomorphic variables that can be obtained from aerial photographs or topographic maps and reduced that number to 8 key geomorphic variables. A discriminant model is used, with the eight variables as input, to give a value that enables a particular stream to be categorized as either a "good" or "poor" salmon producing habitat. Intermediate quality streams can not be categorized. This technique is straightforward and relatively objective in both data collection and analysis. Theoretically, it can be applied anywhere for spawning habitat, although individual variables might need to be modified, added to, or deleted.

McConnell et al. (1982) developed an analytic procedure for predicting the habitat quality and fish species occurrence in planned reservoirs. This "pattern recognition" procedure involves developing a five-digit number, where each digit represents an aggregate of habitat attributes. The aggregate attributes are temperature, mineral turbidity, structure (cover, rocks, etc.), severity of water level fluctuation, and occurrence of shallow, protected coves (a function of mean depth and shoreline development). The digits, representing one of these aggregate attributes, range from 1 to 3. Rules were established for evaluating the five-digit number for a particular planned reservoir. Some subjectivity may exist in the use of these rules. The output of the procedure is a list of fish species that would be expected to exist in the reservoir, at some unspecified time, during the life of the reservoir, assuming those species had access to or were planted into the reservoir.

None of the habitat prediction procedures discussed previously can serve as an intermediate step to predicting population quantities. There is a need to develop procedures that quantify the relationship between the habitat quality and population quantities.

Population Quantities Estimation

Total Population Quantities

Prediction of population quantities has not developed much beyond identifying input variables. The only generic procedures available are simple or multiple regression analyses. Few attempts have been made to develop analytic techniques to predict population quantities over any time interval. Efforts to develop analytic procedures to predict present population quantities have usually included a search for and testing of variables. The selection of variables to be tested has usually been based on previous research and assumes that the variables have a biological and/or ecological relationship to aquatic wildlife and fish quantities. The relationship between variables and population quantities has been developed most often with correlation and regression analyses. Factor analysis has also been used with regression analyses (Harshbarger and Bhattacharyya 1980).

The geographic scope of the techniques varies, with most of them applicable to the local level. Most techniques deal with lakes and ponds, where it is easier to identify key variables and to determine interactions of components within the system, because lakes and ponds are relatively closed systems with sharper boundaries than rivers and streams.

A wide range of species are included, with emphasis on commercial and game fish. Research on invertebrates generally has centered on insects in streams or zooplankton in lakes, ponds, and reservoirs.

Binns and Eiserman (1979) and Burton and Wesche (1974) developed procedures for streams where trout populations are assumed to exist. Inputs to the analyses are primarily abiotic habitat factors.

Binns and Eiserman, working with 36 Wyoming streams, originally developed a technique that requires the use of 10 factors: late summer stream flow, annual stream flow variation, maximum summer stream temperature, nitrate nitrogen, fish food abundance, fish food diversity, cover, eroding stream banks, water velocity, and stream width. Because of the difficulty of processing macroinvertebrate samples to determine fish food abundance and diversity, those factors were replaced with vegetation abundance on the stream substrate. Fish food abundance and diversity is considered a function of this substrate factor. Field measurement values for the various factors are converted to rating values that are then used in multiple regression analyses to develop predictive equations for trout standing crop.

Burton and Wesche (1974), working on nine Wyoming streams and rivers, developed a technique that uses multiple and simple linear regression analyses to identify watershed and streamflow factors significantly related to estimates of trout standing crop. Four of these factors (watershed drainage basin area, mean drainage basin elevation, drainage basin forested area, and total drainage basin stream length) are used to develop a potential productivity index equation.

Most techniques for estimating fish population quantities for lakes, reservoirs, and ponds estimate fish production or fish standing crop. Fish yield or harvest, expressed in kilograms per hectare per year or pounds per acre per year, obtained from sport or commercial fisheries catch, is used as an index of fish production. Various inventory techniques used to estimate fish standing crop (expressed in kilograms per hectare or pounds per acre) include draining the body of water, killing the fish with poison, using mark and recapture methods, or netting intensively. Variables used to estimate fish production or standing crop include lake area, age, maximum depth, mean depth, shoreline development, outlet depth, water level fluctuation, storage ratio (ratio of water body volume to average annual discharge), carbonate concentration, total dissolved solids, and growing season. Simple linear or multiple regression are used to relate these variables to fish production or fish standing crop.

Rounsefell (1946) used regression analysis to correlate lake surface area to sport fish yield, commercial fish yield, and total population. He found that as lake size increase, both fish yield and total population per acre decline. The lakes he studied range widely in size and geographic location in North America.

Carlander (1955) reevaluated the data used by Rounsefell (1946) and grouped the lakes by geographic area. He showed a negative correlation between standing crop and maximum depth in cold and warm water lakes. He also found a positive rather than negative correlation between lake area and fish standing crop for four of the five lake groups. Carlander suggested that Rounsefell's findings may be an indication of fishing effort per acre rather than fish production. Ryder et al. (1974) points out that it is generally accepted that small lakes are exploited more efficiently per unit surface area than are large lakes, when both are subjected to proportionally similar fishing efforts.

The relationship between lake water total mineral content and fish production was considered by Carlander (1955) and Rawson (1951). Carlander also related maximum lake depth with fish standing crop and showed a negative correlation between standing crop and maximum depth for trout. Carlander, using Rounsefell's (1946) data showed a positive correlation between carbonate concentration and fish standing stock in cold and warm-water lakes, and reservoirs. Rawson proposed that total mineral content provides a simple and useful indicator of edaphic conditions related to lake productivity. He cautioned that differences in productivity can not be ascribed to mineral content alone. Rawson (1951) suggested that lake morphometry is a more important factor. Rawson (1952) later investigated the relationship between mean depth and fish production (based on 25-year average catch) in 13 large North American lakes (surface area ranged between 460 and 31,820 square miles) and showed that the correlation was negative, thus emphasizing the importance of shallow water to lake productivity.

Hayes and Anthony (1964) showed a high correlation, using multiple regression, between fish productivity and a combination of lake area, lake mean depth, and methyl orange alkalinity. Ryder (1965) proposed a morphoedaphic index (MEI) for predicting the potential fish production of north-temperate lakes in North America. He used published data on 34 lakes and simple linear regression to establish this relationship. His morphoedaphic index is as follows:

$$\text{MEI} = \frac{\text{total dissolved solids (p/m)}}{\text{mean depth (feet)}}$$

Ryder et al. (1974) reviewed the literature relating to the development and subsequent use of the morphoedaphic index as an indicator of fish yield. He discussed the work of Jenkins (1968), who used multiple regression techniques to relate biomass yield for 210 temperate and south-temperate reservoirs in the United States to several abiotic factors. The four major multiple regressions completed by Jenkins were (1) standing crop on the morphoedaphic index; (2) standing crop on total dissolved solids; (3) sport fish harvest on total dissolved

solids, growing season, age, area, and shore-line development; and (4) commercial harvest on growing season, mean depth, storage ratio, age, and water level fluctuation. Jenkins concluded that the most meaningful regression was that of standing crop on the morphoedaphic index. Ryder et al. (1974) suggested that the lower efficiency of the MEI that was obtained with Jenkins' reservoir systems, compared with the results Ryder (1965) obtained for north-temperate lakes, was partly a result of the difference between reservoirs and lakes. They pointed out that reservoirs tend to be flowing water systems much more than do lakes. Many reservoirs have relatively low volumes and high flushing rates that result in a different type of primary production and energy flow system from that of lakes.

In a study of 20 Oklahoma reservoirs, more than 200 ha in area, Jenkins, (1976) using correlation and regression analysis, found storage ratio (the ratio of the reservoir volume at average pool to the annual discharge volume) to be the most important independent variable when regressed against fish standing crop. Other independent variables tested were: surface area, mean and maximum depth, outlet depth, shoreline development, growing season, water level fluctuation, total dissolved solids, and age of reservoir.

In another effort, Jenkins (1977) studied 166 reservoirs; all were more than 200 ha and all but six are south of the Mason-Dixon line and east of 100° W longitude. The reservoirs were divided into two major groups and into four subgroups. Hydropower and nonhydropower reservoirs were the major groups. The hydropower reservoirs are separated into mainstream (storage ratio less than 0.165) and storage reservoirs. The nonhydropower reservoirs were divided according to their water chemistry: those exhibiting dominant carbonate-bicarbonate ions and those exhibiting dominant sulfate-chloride ions. Jenkins used correlation and stepwise multiple regression analyses. The dependent variable was fish standing crop; the independent variables were reservoir area, age, mean and maximum depth, water level fluctuation, outlet depth, thermocline depth, growing season length, total dissolved solids, shore-line development, and storage ratio. Partial correlation analysis consistently showed total dissolved solids to be the most important independent variable.

Matuszek (1978) analyzed data from 22 large North American lakes and basins (surface area ranged from 187 to 82,414 km²) that had been moderately to intensively fished. He estimated the maximum sustained fish yield (MSY) for these lakes and used simple linear and stepwise multiple regression to test the relationship between MSY and abiotic and biotic independent variables. The independent variables he used were mean depth, total dissolved solids, morphoedaphic index, and bottom fauna standing crop. The highest coefficient of determination occurred for MSY and bottom fauna standing crop. A multiple regression of mean depth and total dissolved solids with MSY and a regression of MSY with the morphoedaphic index had slightly lower coefficients of determination.

Oglesby (1977) related fish yield to lake phytoplankton standing crop, primary production, and to the morphoedaphic index. The lakes he included were in North America, Great Britain, Europe, Africa, and Asia. He studied lakes ranging in size from 1 to 82,417 km². Using simple linear regression, he obtained the best fits for fish yield on summer phytoplankton standing crop for 19 lakes. A good correlation resulted from the regression of phytoplankton primary productivity on fish yield for 15 lakes. The regression of the morphoedaphic index on fish yield gave a lower coefficient of determination when 17 large lakes were included.

The relationship between primary production and fish yield has also been shown by other investigators. Hrbâĉek (1969) analyzed the data of Lyakhnovich et al. (1964) and found a good relationship between planktonic primary production and crop yield. McConnell et al. (1977) conducted experiments in small, artificial ponds. The ponds ranged in size from 0.001 to 0.1 ha, and were from 0.74 to 1.5 m deep. The ponds were inoculated with seston concentrates and macrophyte washings from several natural ponds. Fish species were tilapia hybrids, trout, goldfish, and a combination of tilapia hybrids and channel catfish. Fish yield was based on growth over the experimental period and expressed as grams per square meter per day. Simple linear correlation showed a good relationship, for all ponds taken together, for fish growth related to gross primary production in the ponds.

Aggus and Morais (1979) used multiple regression analyses to relate several independent variables to total fish standing crop and to standing crop of each of 14 different groups of fish (e.g., clupeids, carp, minnows, walleye, sportfishes). Those regressions were developed for 228 reservoirs in the United States, larger than 200 ha, in area at normal pool. The reservoirs were divided into those having (1) a thermocline; (2) dissolved solids composed of calcium-magnesium, carbonate-bicarbonate; (3) dissolved solids composed of calcium-magnesium, sulfate-chloride; (4) dissolved solids composed of sodium-potassium, carbonate-bicarbonate; or (5) dissolved solids composed of sodium-potassium, sulfate-chloride. The reservoirs were further classified as (1) hydropower storage; (2) hydropower mainstream; (3) nonhydropower; (4) reservoirs smaller than 70,000 acres, with total dissolved solids less than 600 p/m and growing season greater than 140 days; or (5) hydropower reservoirs in the Great Smoky, Ozark, and Ouachita Mountains. The independent variables for a reservoir were its age, area, mean depth, outlet depth, water level fluctuation, shore development, growing season, total dissolved solids, and storage ratio. The stepwise regression method of maximum r^2 improvement (Barret al. 1976) was used to develop the best 1-, 2-, 3-, or 4-variable regression models.

Schueler and Sullivan (1967) quantified the potential commercial fish production in the midwestern United States. They estimated acres of commercial fishery habitat (lakes, reservoirs, and rivers) for the Upper and Lower Mississippi, Ohio, Missouri, Arkansas-White-Red, Red River of the North and Tennessee river basins. Fish standing crop classes were identified with an average standing crop value for each class. The estimated acreage for lakes and reservoirs in each river basin in the study, representing each standing crop

class, was tabulated. Total annual potential production of lakes and reservoirs, assuming potential production to be 25% of standing crop, was developed by standing crop classes. For rivers, an arbitrary standing crop value was assigned and the same 25% of standing crop was assumed to be the potential production. From known river commercial fishery acreages, total river production was estimated. The estimated potential production (lbs/acre) was compared with actual harvest figures.

Most techniques for predicting aquatic wildlife and fish population quantities as output emphasize identifying the key variables that can be used to predict the output. In almost all cases, the analytic procedures to predict aquatic wildlife and fish production are simple or multiple regression techniques. The techniques are primarily local in scale and do not have the capability to make predictions over time. One exception is Ricker (1971). He presented techniques for estimating fish production in fresh waters, including both lakes and rivers. Ricker's techniques deal with varying time and geographic scale and use various types of mathematical procedures, including calculus.

Another procedure which makes predictions over time is the model of fish biomass dynamics developed by Kitchell et al. (1974). This is an attempt to provide an ecologically meaningful model by including aspects of physiology, population biology, and trophic ecology. The model is based on principles derived from many studies of many species in addition to fishes. It was tested, using data on the bluegill (*Lepomis macrochirus*).

There have been several efforts to develop complex models to simulate varying portions of aquatic ecosystems. Prediction of population quantities over time can also be made with these models for the ecosystem components included. One example is the model of the pelagic zone ecosystem of Lake Wingra, Wisconsin (MacCormick et al. 1974). This model has seven compartments: phytoplankton, zooplankton, benthos, suspended organic detritus, permanent sediment, geologic sediment, and dissolved organic matter. The six model interactions are excretion and egestion by zooplankton, benthic insects, and fish; respiration and nonpredation deaths; reproduction; emergence of benthic insects; decomposition; and sedimentation. The input forcing functions are primary production by phytoplankton, and dissolved and detritus organic matter carried by wind and water currents from littoral zones to the pelagic zone and from storm sewers and runoff from terrestrial zones. Outputs from the model are losses of carbon and energy caused by respiration and losses of carbon andenergy to deep geologic sediment. The loss of suspended and dissolved organic matter carried by water flowing out of the lake is assumed to be negligible.

The model of a cove of Lake Texoma, Texas-Oklahoma (Patten, Egloff, Richardson 1975) is extremely detailed and attempts to include every conceivable aspect of the cove ecology. Two of the objectives for this effort were to understand the interrelationships of the cove ecosystem as an ecological unit and to examine the basis in these interrelations for responses to selected small, but realistic perturbations.

The phytoplankton-zooplankton-nutrient interaction model for Western Lake Erie (DiToro, O'Connor, Thoman 1975) was constructed to provide an aid in understanding and management of eutrophication. It contains compartments for zooplankton and phytoplankton allowing predictions of the biomass of these groups of organisms over time.

A final example of this type of complex aquatic ecosystem simulation model is the Lake Washington model (Chen and Orlob 1975) which includes compartments for, among others, algae, zooplankton, benthic animals, and fish. Biomass for those groups of organisms can be projected over relatively short periods of time (i.e., up to 1 year).

Harvest Population Quantities

An important fish management concern has to do with the relationship between the amount and kind of the harvest population and the response of ecosystems to that removal. As a result, numerous ecological analysis techniques have been developed for estimating the fraction of the total population that makes up a harvest population.

One harvest concept assumes that the production of an ecosystem can be partitioned into fractions. One fraction must remain in the ecosystem to maintain the structural and functional integrity and the productive capability of the ecosystem over time, while another fraction or maximum quantity is that which can be safely harvested. This is referred to as the maximum sustained yield (MSY) approach to fish harvest. Most analytic techniques to quantify the harvest of fish have been for single species of marine and large-lake fish populations.

Larkin (1977, 1978), Holt and Talbot (1978), and Caughley (1977) found major problems with the concept of MSY and the techniques for calculating MSY that relate to the larger problem of removal. MSY deals with the "dynamics of particular species or stocks without explicit regard to the interaction between those species or stocks and other components of the ecosystem" (Holt and Talbot 1978). For example, MSY does not deal with the facts that fish food webs, especially, are highly complex and each species both feeds upon and serves as food for several other species. MSY fails to account for the highly flexible fish growth rates which can change drastically as fish either gorge themselves or withstand starvation. Furthermore, life history events, such as maturity, are usually related to size rather than age. Maximum sustained yield is concerned only with the quantity and not the quality of the potential yield from the ecosystem. MSY also depends on a degree of stability and resilience of the resource that may not exist. Various changes in the system (e.g., change in species composition, proportion of predators to prey, size distribution of reproducing animals and resultant change in quality and quantity of eggs or young pro-

duced) or changes in external factors, such as climate, can significantly affect actual, compared to calculated, maximum sustained yield.

Thus, while an elaborate mathematical methodology has been developed for estimating maximum sustained yield for marine and large freshwater lake fisheries, a measure of the effects of this kind of harvest on all species of fish has not been developed for an entire ecosystem.

Despite its limitations MSY probably is useful as a first rough estimate of safe harvest amount for major commercial species. Many of the techniques for estimating MSY were developed to predict the effects of fishing on marine fish populations (Schaefer 1968, Schaefer and Beverton 1963, and Ricker 1958, 1975). Ricker (1971) presents the techniques for estimating harvest as well as fish production in fresh waters. Most of the techniques deal only with one species at a time and do not consider two or more interacting species. The fish system is generally considered to be in a state of dynamic equilibrium with average environmental conditions. The techniques also consider that the fish stock (biomass) of harvestable size is increased by the addition of recruits (results from reproduction) and by growth of the individuals in the stock; and fish stock is decreased by natural deaths and by the amount of fish taken by the fishery. It is assumed that for a fish population to maintain a state of dynamic equilibrium, there must be a homeostatic mechanism that, if mortality increases, either growth or recruitment will increase to compensate for the loss and bring the population back to the equilibrium level.

Two basic approaches have been taken in the various fisheries MSY models. One is called the "logistic model" approach associated with Schaefer (1954, 1957; the other is the "dynamic pool model" approach associated with Beverton and Holt (1957). Each of these approaches was originally developed for a specific fishery that imposed unique data limitations; each fishery, therefore, required unique assumptions.

Schaefer (1957), in developing the logistic model, was concerned with establishing the relationship between catch and fishing effort in the Pacific tuna fishery. Good statistics of catch and effort were available, going back to near the time when the fishery first started. Thus, the data covered the critical period when the population was close to its unfished equilibrium state. In his model, he combined the terms recruitment, growth, and natural mortality into one term: a "coefficient of population increase" as a single function of population size. Shaefer's model assumed that (1) the rate of natural increase responds immediately to changes in population density (i.e., time lags are ignored; this can be done where the rate of fishing effort change is slow, and/or when the life span of the fish is sufficiently short); (2) the rate of natural increase at a given weight of population is independent of any deviation in the age composition of the population from the steady-state age composition at that population weight; and (3) the fishing mortality rate is proportional to fishing effort. His model predicted catch from (1) the environmentally-limited (unfished) upper value of the average population size; (2) the biomass of the fishable part of the population; and (3) the fishing effort. Provisions were included to deal with nonequilibrium conditions.

Beverton and Holt (1957) were concerned with techniques for assessing regulation on North Sea bottom-dwelling fisheries such as plaice and haddock. The investigators were concerned primarily with the effect of mesh size regulation but also had to consider the effect of changes in fishing effort. Some good catch and effort data were available, although important early data did not exist. Extensive age-composition data were available because age determination for these species is relatively easy. Thus, in the dynamic pool model, the assumptions are (1) equilibrium or steady-state conditions prevail, (2) a constant number of recruits enter the fishable stock each year, (3) the natural mortality coefficient is constant, (4) the length of a fish increases in proportion to its age and its weight varies as the cube of its length (growth), and (5) the relationship between fishing effort and fishing mortality is proportional. Beverton and Holt also assumed that the rates of recruitment, natural mortality, and growth are density independent. The model, using differential equations, computed equilibrium catch for various values of fishing mortality; it also predicted the effect on equilibrium catch as a result of a change in selectivity of the fishing gear and amount of fishing.

Anderson (1974) developed a simplified technique for estimating largemouth bass production and sustained harvest. This technique is based on a procedure originally developed by Allen (1950, 1951). It uses a graphic model that plots the number of fish as a function of average weight for the life span of a year class. The area under the curve (an approximate integration of growth and mortality rates) is an estimate of production during the life span of the year class. The area under the curve is also an estimate of annual production of the population if the population is in a steady state or if average growth rate and age distributions can be estimated. Potential harvest is defined as the total weight of fish of harvestable size that die each year. Potential harvest also can be estimated from the graph. Anderson assumed (1) the average age distribution, growth rate, and recruitment rate are in a steady state; (2) the annual production equals annual loss from mortality; and (3) growth and mortality are proportional (i.e., all mortality occurs during the growing season).

All of these approaches include only population quantity, structure and dynamics variables. Leslie matrixes (Leslie 1945; Usher 1972, 1976; Jensen 1971; Van Winkle et al. 1974, 1978) may provide a means for relating environmental effects to the population dynamics of fish.

Using rapid analog and digital computers, simulation models of fisheries have been developed to study the effects of effort control on abundance and yield of exploited fish populations. Most of these simulation models deal with commercial marine fisheries. Of the models discussed, only those of Walters (1969) and Orth (1979) apply strictly to fresh water species.

Silliman (1967) used analog computers to simulate the results of the New England cod fishery from 1932 through 1958. Paulik and Bevan (1963) modeled the sockeye salmon in the Puget Sound region between the time a group of mature fish entered the Sound from the open ocean until they arrived on the spawning grounds. Schaefer (1967) applied the Beverton-Holt dynamic pool model to develop a simulation model for estimating the effects of varying fishing regulations on the Peruvian anchoveta fishery.

Silliman (1966, 1969) developed simulation models for use with analog computers to derive data on population dynamics of whales. He also demonstrated the model for Pacific sardine, haddock, Atlantic cod, lake trout, skipjack tuna, bigeye tuna, blue whale, and fin whale. Forecasts of sustainable catch were made for the two species of tuna and the fin whale. Using Voltera equations to generate the biomass of one population as a function of the biomass of the other, he also modeled two competing populations. These models were applied to data of the competing pairs: Pacific sardine-northern anchovy, and the yellowfin tuna-skipjack tuna.

Walters (1969) used digital computers to develop a simulation model for fish population and maximum yield.

The model used age-specific natural mortality rates, growth rates, relative fecundities, and any desired stock-recruitment relationship. The model found solutions for density, growth, and yield by age group and joins age groups over time to predict yield. Orth (1979) developed a simulation model that predicts year-class strength, production, and yield of the freshwater largemouth bass. The model, which was age-structured and deterministic, has numbers, average weights, average lengths, biomass, yield in weight, yield in numbers, growth, and net production as state variables. Mortality from egg to age class I is estimated with a multiple regression equation that uses water level during spawning and water level fluctuation since the end of the previous growing season as independent variables.

Numerous sophisticated procedures have been developed to estimate maximum sustained yield. Almost all of these techniques are designed for single species stocks of animals (mostly marine fish). Some major assumptions are made because much of the needed information usually is not available. These assumptions can be sources of error in the predictions. No adequate techniques exist to define or predict the effect on an ecosystem of harvesting a part of that ecosystem.

MULTIRESOURCE INTEGRATION APPROACH

Techniques are needed to integrate planning for wildlife and fish resources with planning for other natural resources. Much work also is needed using integrated analysis research to determine if the output of the individual resource or functional analyses reviewed earlier can be incorporated into multiresource ecological analysis models.

A few existing techniques approach an integrated analysis of resources; however, they are still very much in the developmental stages. DYNAST (Boyce 1977) is an example of a technique that begins to address integrated ecological analysis of resources. Only the wildlife and fish components of this model were evaluated.

DYNAST considered timber, water, esthetics, and wildlife components. The wildlife submodel only addressed habitat quality and was highly subjective, relying heavily on expert opinion.

CONTINUING RESEARCH AND DEVELOPMENT NEEDS

More research is needed on the wildlife and fish resource aspects of the renewable resource, planning process. Research also is needed where economic and social analyses are fully integrated with ecological analyses. All spatial hierarchical levels should be included also.

Specifically, there is a critical need for procedures that objectively select, integrate, and further process the wildlife and fish resource analysis outputs for use as inputs to integrated planning models. Methods are needed to objectively select, from the many possible combinations of multiresource management practices, those practices or combinations that most benefit wildlife and fish, and other natural resources. Procedures are needed to objectively identify the ecosystem processes affected by the various management practices applied. The response of wildlife and fish resources to these management practices over various time and spatial scales also should be quantified. A procedure for determining the priority of species to be considered in ecological analyses also should be developed. This requires the development of criteria for establishing a priority for ecologically, economically, and socially important species. Improvement of the capability of techniques to estimate species population occurrence and quantities over various time and spatial scales also is important. Finally, techniques are needed, which apply to more species, and which estimate population structure and dynamics for various time and spatial scales.

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Rocky
Mountains

Southwest

Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526